

Fågelinventeringar - metoder och tillämpningar

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Föreliggande avhandling grundar sig på följande nio separata uppsatser:

1. Svensson, S. 1974. Interpersonal variation in species map evaluation in bird census work with the mapping method. *Acta Ornithologica* 14:322-338.
2. Enemar, A., Sjöstrand, B. and Svensson, S. 1978. The effect of observer variability on bird census results obtained by a territory mapping method. *Ornis Scandinavica* 9:31-39.
3. Svensson, S. 1979. Census efficiency and number of visits to a study plot when estimating bird densities by the territory mapping method. *Journal of Applied Ecology*, in print.
4. Svensson, S. 1978. Förenklad revirkarteringsmetod för inventering av fåglar på myrar och mossar. *Vår fågelvärld* 37:9-18.
5. Svensson, S. 1978. Efficiency of two methods for monitoring bird population levels: Breeding bird censuses contra counts of migrating birds. *Oikos* 30:373-386.
6. Svensson, S. and Carlsson, U. T. 1979. Structure and dynamics of an alpine bird community. (Manuscript).
7. Svensson, S. 1978. Territorial exclusion of *Acrocephalus schoenobaenus* by *A. scirpaceus* in reedbeds. *Oikos* 30:467-474.
8. Svensson, S. 1978. Storlek och isolering hos naturreservat: synpunkter på tillämpning av ekologisk teori. *Anser*, Supplement 3: 225-234.
9. Svensson, S. 1977. Land use planning and bird census work with particular reference to the application of the point sampling method. *Polish Ecological Studies* 3:99-117.

I uppsats nr 1 görs en jämförelse mellan olika personers resultat vid utvärdering av en uppsättning identiska artkartor hämtade från revirkarteringar utförda inom Svenska häckfågeltaxeringen. Betydande skillnader registrerades mellan olika personer vad gäller extremvärdena. I genomsnitt för de sex arter som ingick i försöket uppmättes variationskoefficienter på drygt 20 procent. Majoriteten av försökspersonerna föll dock inom ett rätt måttligt intervall. Försöket visar att det är väsentligt att det finns en central kontroll av artkartorna inom större inventeringsprogram så att en likartad utvärdering säkerställs. Naturligtvis är det en ganska artificiell och svår situation som en person ställs inför i ett försök som detta. Erfarenheter från det självupplevda fältarbetet tillsammans med kännedom om provytans biotoper bidrar i hög grad till att underlätta utvärderingen. Man bör därför kunna förvänta sig betydligt bättre resultat från inventerarnas egna utvärderingar av sina provytor. Det är därför tillfredsställande att notera i siffermaterialet att medelvärdet för försökspersonerna nästan undantagslöst överensstämmer väl med vad inventeraren själv för respektive yta kommit fram till. Min egen oberoende utvärdering av artkartorna överensstämmer dessutom med båda dessa värden.

För att närmare studera vilka skillnader som uppstår mellan olika personer som inventerar samma provyta samtidigt genomfördes ett experiment i en björkskogsyta i Ammarnäs (uppsats nr 2). I detta experiment genomförde var och en av de fyra deltagarna sitt inventeringsarbete oberoende av de övriga deltagarna. Var och en gjorde en egen utvärdering av sina artkartor, en utvärdering som senare kontrollerades av samtliga deltagare för att säkerställa att den varit likartad. I detta experiment är det således i första hand skillnader i insamlandet av fältdata som testas. Resultatet blev mycket tillfredsställande. Skillnaderna mellan observatörerna var överlag obetydliga. Värt att notera är dock att det rörde sig om tränade observatörer. Förmodligen skulle större skillnader ha uppträtt om observatörerna inte haft tidigare erfarenhet av eller tidigare samarbetat med revirkarteringar. Vad gäller arbete inom inventeringsprogrammet i Ammarnäs kan vi dock notera att byte av personal i provytorna inte nämnvärt påverkar möjligheterna att följa beståndsförändringarna.

Inventeringseffektiviteten, dvs. chansen att registrera en i provytan befintlig fågel, varierar med tidpunkt, art, mm. Effektiviteten är av särskild betydelse för att bestämma vilket minsta antal besök som krävs för att en inventering skall ge ett tillfredsställande resultat. I uppsats nr 3 ges en översikt av hur olika effektiviteter påverkar behovet av inventeringar. Utgångspunkten är att jag anser att det i ett revir bör finnas minst tre observationer för att man skall räkna det som 'permanent' bebott. Genom teoretiska beräkningar visar jag att med 8-10 besök är det svårt att uppfylla detta krav för arter med inventeringseffektiviteter som väsentligt understiger c. 50 %. Att öka antalet besök är ofta inte möjligt av resursskäl. Min slutsats blir därför att man måste sträva efter att höja inventeringseffektiviteten till en sådan nivå att man med 8-10 inventeringar får de behövliga tre registreringarna för flertalet revir. Detta kan ske på två sätt, nämligen dels genom att optimera tidpunkterna för besöken och dels genom att förlänga tiden för de enskilda besöken, vilket tillåter ett noggrannare sökande efter fåglarna. Denna rekommendation ges främst med tanke på omfattande inventeringsprogram av typ Svenska häckfågeltaxeringen, där ett stort antal amatörer är involverade. För dem är det väsentligt att kunna genomföra inventeringen med så få besök som möjligt. Det är en mindre belastning att vid varje besök arbeta noggrannare än att öka antalet besök.

Kravet att en inventering skall kunna genomföras med så liten arbetsinsats som möjligt har lett fram till studier av möjligheterna att minska antalet besök i förhållande till vad som krävs enligt Internationella fågeltaxeringskommitténs standard (8-10). I enkla biotoper med hög häckningssynkroni för de ingående arterna bör detta vara möjligt. I uppsats nr 4 visar jag att man kan minska antalet besök till fem vid inventering av myrar och mossar. Redan tidigare har fem besök använts vid inventering av särskilt fågelfattiga fjällhedar (uppsats nr 6). När man inventerar vissa speciellt lättinventerade arter och inte strävar efter att uppskatta hela fågelsamhället kan antalet inventeringar minskas ytterligare.

Inventeringarna inom Svenska häckfågeltaxeringen syftar ytterst till att följa olika arters beståndsförändringar i landet. Det finns dock andra metoder som kan användas för samma ändamål. I uppsats nr 5 görs en jämförelse mellan olika tillvägagångssätt: häckfågeltaxeringar jämförs med räkningar av antalet för ringmärkning fångade fåglar och med antalet översträckande fåglar vid fågelstationer. Resultatet blir att det i regel är säkrare att basera beståndsovervakning på häckfågeltaxeringar. Skälet är den stora mellanårsvariation som uppträder såväl i totalsiffrorna för antalet fångade fåglar som i motsvarande siffror för antalet översträckande. För vissa arter, närmare bestämt några inomeuropeiska flyttare, noteras dock tämligen god överensstämmelse mellan häckbestånd och antalet flyttare. Värt att notera är i detta sammanhang den goda korrelationen mellan antalet

häckande ängsbiplärkor i provytorna i Ammarnäs och totalantalet ringmärkta ängsbiplärkor i landet (uppsats nr 6).

Noggranna och framför allt mångåriga inventeringar ger unika möjligheter att i detalj studera fågelsamhällens struktur och dynamik. En sådan undersökning är den som beskrivs i uppsats nr 6. Här redovisas resultaten från 15 års inventeringar i två fjällhedsprovtytor i Ammarnäs. Fjällhedens fågelsamhälle är artfattigt och domineras av en handfull arter med ängsbiplärka och lappspurv i topp. Under de femton åren har en hel del variationer i abundans och artsammansättning ägt rum, men de långsiktiga trenderna är obetydliga. Det mest remarkabla som skett är en nedgång i antalet ängsbiplärkor. Som helhet har fågelsamhället blivit något artfattigare men framför allt individfattigare samt därmed fått ökad Shannonsk diversitet samt en jämnare fördelning av individerna på de olika arterna. Strukturen i samhället har jämförts med olika teoretiska art-abundansmodeller och befunnits kunna bäst beskrivas med en geometrisk serie. Detta tyds som att fågelsamhället har karaktären av pionjärsamhälle underställt ett fåtal dominerande omvärldsfaktorer, av vilka det kärva klimatet säkert är mycket betydelsefullt.

Fågelinventeringar ger möjlighet inte bara till studier av hela samhällens struktur och dynamik utan även till detaljerade analyser av enskilda arters förhållande. Ett av de mest kontroversiella och svåraste problemen inom ekologin är att påvisa och kvantifiera konkurrens mellan arter. Revirkarteringar av bl. a. sävsångare och rörsångare i Silvåkrakärret i Skåne producerade utan att det var planerat intressant och användbar information i detta avseende (uppsats 7). Det visade sig nämligen att redan etablerade sävsångare trängdes undan av senare anländande rörsångare i vass, som är den senare artens optimalbiotop. Andra författare har redan tidigare noterat revirförskjutningar hos sävsångare när rörsångare anlönt, men i Silvåkrakärret var det uppenbarligen fråga om ett nästan fullständigt bortträngande av sävsångarna. Om dessa inte för någon annanstans och häckade måste rörsångarnas närvaro vara en ytterst betydelsefull faktor när det gäller evolutionen av sävsångarens nisch. Detta intressanta artpar torde vara ett mycket lönande objekt för framtida konkurrensforskare.

Många olika typer av fågelinventeringar utförs i Sverige och annorstädes, och många av dem syftar direkt till att klarlägga problem inom det praktiska naturvårdsarbetet. Naturvård har länge varit en teoretiskt svagt förankrad verksamhet, trots att den under senare decennier inrangerats bland allt annat under ekologiparaplyn. Under senare år har dock en rad intressanta arbeten producerats, där man försöker tillämpa erfarenheter från den teoretiska ekologin på praktisk naturvård. Inte minst öbiogeografin har bidragit till detta. I uppsats nr 8 belyses med några exempel hur främst storleken på olika biotopområden påverkar fågelfaunans sammansättning och arternas chanser att leva kvar. För att bevara en artrik fågelfauna i skånska skogsområden krävs att dessa är av rätt betydande storlek, gärna över 50 kvadratkilometer om de ligger isolerade från andra större skogar. Skälet till att artrikedomen minskar med minskande areal på ett skogsområde är att vissa bestämda arter försvinner när området understiger en viss gräns, olika för olika arter, samtidigt som nyrekryteringen blir svårare ju mindre området är. Ett viktigt skäl till att arter försvinner är att små bestånd är utsatta för stor risk att dö ut av en slump. Riskerna i detta avseende belyses med kärrsnäppan som exempel. Denna arts biotop har i våra dagar en mycket fläckvis fördelning i Skåne och många lokala bestånd är synnerligen små. Det visas att ett kärrsnäppebestånd om färre än 10 par har låg överlevnadschans på sikt om inte påfyllning från andra bestånd kan ske.

De fågelinventeringar som görs inom den praktiska naturvården syftar ofta till att skapa underlag för fysisk planering. En metod som kommit till användning i rätt stor skala härvidlag är punkttaxe-

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ringsmetoden. Med denna metod kan man nämligen översiktligt inventera rätt stora områden till rimliga kostnader. Metoden är dock i likhet med linjetaxeringar betydligt känsligare för diverse felkällor än revirkarteringar. I uppsatsen påvisas framför allt den stora påverkan på resultaten som tidpunkten på dagen och under säsongen har. Även personskillnader påverkar resultaten i hög grad. Till skillnad från vid revirkarteringar har man under punkttaxeringar inga möjligheter att modifiera sitt inventeringsarbete efter den egna förmågan. Man har att räkna fåglar under en viss tid vid varje punkt oberoende av svårigheterna. Det är därför synnerligen väsentligt att de deltagande personerna i ett större projekt är jämförbara.

Avhandlingen berör som framgått av ovanstående sammanfattning en rad olika frågor av såväl teoretisk som praktisk natur. Avslutningsvis kan det vara lämpligt att se litet in i framtiden. Vilka typer av fågelinventeringar är mest angelägna att driva i fortsättningen. Vid den genomgång av litteraturen som jag gjort främst i anslutning till uppsats nr 6 har jag funnit att inventeringar som sträcker sig över mycket långa tidsperioder är en bristvara. Det finns rätt gott om inventeringar som täcker perioder om c. 5 år eller något mer. Men det är ytterst få som täcker flera decennier. Detta är i och för sig naturligt eftersom enskilda individer sällan har möjligheter att bedriva arbete med så långa tidsperspektiv. Men det är ytterst beklagligt eftersom många ekologiskt betydelsefulla händelser sannolikt inträffar med mycket låg frekvens. Studier av populationer och samhällen över korta tidsperioder, kanske blott enstaka år, kan innebära att man aldrig får möjlighet att registrera effekterna av de faktorer och händelser som kanske egentligen är avgörande för utvecklingen och anpassningen. En avslutande förhoppning är således att mycket långsiktiga, fortlöpande fågelinventeringar kan ges en mera framträdande plats i den framtida ekologiska forskningen.

På metodsidan ser jag främst ett behov av att utveckla en ny och mera flexibel standard för revirkarteringsmetoden, dvs. att vidareutveckla de tankar som lett fram till den förenklade metoden för mossar (uppsats nr 4). Det vore väsentligt att närmare fastlägga omfattningen av den behövliga inventeringsinsatsen i olika biotoper, olika fågelsamhällen och i regioner med olika utdragen häcknings-säsong.

Ekonomiskt stöd för olika delar av de studier som ingår i avhandlingen har erhållits från Statens naturvårdsverk, Statens naturvetenskapliga forskningsråd, Sveriges ornitologiska förening, Skånes ornitologiska förening, Magnus Bergwalls stiftelse samt Lunds universitet.

Många personer har på olika sätt bidragit till studiernas tillkomst, inte minst de många inventerare som helt ideellt insamlat fältdata. Ett alldeles speciellt tack vill jag rikta till två personer, nämligen professorerna Per Brinck och Anders Enemar. Den förstnämnde har under årens lopp på ett utomordentligt sätt stött min verksamhet och alltid sett till att nödvändiga resurser stått till förfogande. Den senare har varit en källa till ovärderlig stimulans särskilt i det arbete som bedrivits inom Luvre-projektet i Ammarnäs. Jag vill också rikta ett varmt tack till mina kolleger och vänner såväl vid institutionen i Lund som i Luvre-teamet. Utan den angenäma om än ibland intellektuellt destruktiva miljö som dessa skapat hade forskningsarbetet lätt kunnat bli en börda, vilket det aldrig blivit för mig.

BIRD CENSUSES - METHODS AND APPLICATIONS

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This is a summary of a thesis in Swedish with the title: Fågelinventeringar - metoder och tillämpningar, defended at the Zoological institute, University of Lund, on 23 May, 1979. The thesis (4 pp.) is a brief report on the main ideas and results contained in the following nine papers:

1. Svensson, S. 1974. Interpersonal variation in species map evaluation in bird census work with the mapping method. *Acta Ornithologica* 14:322-338.
2. Enemar, A., Sjöstrand, B. and Svensson, S. 1978. The effect of observer variability on bird census results obtained by a territory mapping method. *Ornis Scandinavica* 9:31-39.
3. Svensson, S. 1979. Census efficiency and number of visits to a study plot when estimating bird densities by the territory mapping method. *Journal of Applied Ecology*, in print.
4. Svensson, S. 1978. Förenklad revirkarteringsmetod för inventering av fåglar på myrar och mossar. *Vår fågelvärld* 37:9-18. (With an English summary: A simplified territory mapping technique for estimating bird numbers on bogs.)
5. Svensson, S. 1978. Efficiency of two methods for monitoring bird population levels: Breeding bird censuses contra counts of migrating birds. *Oikos* 30:373-386.
6. Svensson, S. and Carlsson, U. T. 1979. Structure and dynamics of an alpine bird community. (Manuscript)
7. Svensson, S. 1978. Territorial exclusion of *Acrocephalus schoenobaenus* by *A. scirpaceus* in reedbeds. *Oikos* 30:467-474.
8. Svensson, S. 1978. Storlek och isolering hos naturreservat: synpunkter på tillämpning av ekologisk teori. *Anser*, Supplement 3: 225-234. (With an English summary: Size and isolation of natural reserves: some applications of ecological theory.)
9. Svensson, S. 1977. Land use planning and bird census work with particular reference to the application of the point sampling method. *Polish Ecological Studies* 3:99-117.

Several methodological problems, particularly in relation to the territory mapping technique, are discussed. In paper no. 1 it is shown that different participants in a population monitoring programme may interpret identical species maps in different ways, which necessitates a central control to ensure uniformity and adherence to standards in programmes such as the Swedish Breeding Bird Census. In paper no. 2 it is shown experimentally, on the other hand, that trained observers produce similar results when censusing the same bird community contemporaneously which makes it possible to change observers in long-term census undertakements.

One of the main problems in estimating bird numbers is low census efficiency, caused by generally inconspicuous species or by low song activity at certain times. It is shown in paper no. 3 that problems will appear when the visit efficiency declines appreciably below 50 %. In practice the low efficiency cannot be compensated for by increasing the number of visits. Instead, it is suggested, efficiency should be increased by selecting the times for the visits optimally and by increasing the time for each visit.

It is not only difficult to increase the number of visits to a study plot when a great number of amateurs are involved in a census programme. On the contrary, there is a need to reduce the work investment as much as possible. In simple habitats with high synchrony of breeding among the species this should be possible. In paper no. 4 it is shown that five visits is sufficient to bogs in Sweden.

Counts of breeding birds form the basis of population monitoring programmes in several countries. But there are other potential methods, for example counts of migrants. In paper no. 5 a comparison is made between breeding bird censuses and annual totals of ringed birds and counts of visible migration. It seems that most often breeding bird censuses will produce the most reliable figures, mainly because the migration counts are too variable from year to year to allow early detection of population trends.

Application of avian censuses can be found in many fields, both in theoretical ecology and in practical nature conservation. In paper no. 6 the results of a 15 year study of an alpine bird community are given. It is a species-poor community dominated by a small number of passerines. Its structure indicates strong dependence on a small number of environmental factors. In paper no. 7 the territory mapping technique was used to study interspecific interactions between two warblers. It was found that the reed warbler when it arrives about two weeks after the sedge warbler ousted the latter from territories where this species was already established. In paper no. 8 some results from censuses in woods of different size are used to consider the question of how large a forest reserve in a farmland area must be to ensure the long term preservation of its bird fauna. In Scania isolated woods smaller than about 50 square kilometres will have a clearly impoverished fauna. In the last paper, no. 9, the use of the point count technique for mapping the relative abundance of birds over large areas is discussed. It is particularly the sensitivity of this method to several sources of error that is analysed. It is shown that considerable errors may be introduced because of the variable capabilities of observers, and the variable conspicuousness of birds at different times of day and season.

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STRUCTURE AND DYNAMICS OF AN ALPINE BIRD COMMUNITY

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INTRODUCTION

Habitats that are tree-less because of cold climate are found in two main kinds of land: in lowland tundra with permafrost, and in mountaneous or alpine areas at different elevations depending on latitude. These latter habitats generally do not have permafrost, not even in the vicinity of glaciers. Tundras with permafrost are usually poorly drained while most alpine habitats are well drained. An exception is the bogs and mires that develop on level land and on some slowly climbing slopes.

Some bird communities of tundras and alpine habitats have been studied in the Old as well as in the New World. In this paper we will report results obtained in a study of alpine habitats in Swedish Lapland. The information is important from especially one point of view: the study is probably the longest ever undertaken in alpine habitats since it covers 15 years.

The alpine habitats are usually mosaics of different kinds of heaths, meadows, marshes, mires and bogs. These habitats are at least physiognomically similar to tree-less habitats in the sub-alpine and boreal zones, such as mires and raised bogs. Data from a few such studies have therefore also been included.

Some of the most interesting problems are connected with the structure of the bird fauna and with the long term fluctuations (stability) of it. These questions will therefore be treated in some detail. It is generally assumed that bird populations (as other animal populations) will fluctuate more violently in arctic or alpine habitats than in habitats at lower elevations or latitudes. This assumption cannot, however, be tested since too few multi-year censuses are available from comparable communities under more benevolent climatic conditions.

METHODS

Study plots

The census work was carried out in two study plots, each covering 1 km² (square plots, 1x1 km), about 15 km SSE of Ammarnäs (approximate location of the plots: 65°50' N, 16°20' E). The two plots were located at different elevations. One, the lower plot, called K1, lies about 1 km from the forest line and about 50 m above it. The other, the upper plot, called K2, lies about 3 km from the forest line and at higher elevation.

The lower plot, K1 (800-840 m a.s.l.) is covered by a mosaic of dry scrub heath (with *Betula nana*, *Salix* spp., *Empetrum hermaphroditum*, *Arctostaphylos alpina*, *Vaccinium myrtillus*, and *Juniper communis* as typical components), and mires (with a dominance of *Carex* species). In two parts of the plot mires are more extensive and continuous than elsewhere and in another part the dry heath is rather uniform. There are two small brooks that traverse parts of the plot and along them there are a few small fields of high *Salix* scrub (together less than 1 ha). There are no ponds or lakes within the plot. Parts of the plot are somewhat hilly but the hills are usually lower than 10 m. Dry heath dominate on the hill-tops and mires in between. The plot is typical for one of the main combination of habitats in the Ammarnäs region, covering several hundred square kilometres.

The upper plot, K2, is located about 1 km from K1 on a low mountain ridge (880-940 m a.s.l.). Most parts of K2 are dryer than K1, and the vegetation is poorer. *Vaccinium myrtillus* occurs over most of the plot. In more than half the plot there is no or little scrub. In the lower parts there is some mire vegetation with *Carex* fields and low *Salix* and *Betula* scrub whereas in the dryer parts of the lower levels there are some scattered *Juniperus* stands creeping along the ground. The upper parts are heavily exposed to winds and are also affected by the lack of a thick protecting snow cover in the winter. There are also some parts (2-3 ha) with snow-fields that do not melt away until late in the breeding season, making them unavailable to the birds. The lower parts of K2, between 25-50 ha, are rather similar to parts of K1. The habitats of K2 represent extensive areas of alpine vegetation in the Ammarnäs region; it represents probably the most common type in the low mountains east of the higher Ammarfjället and Tärnafjällen further

west. The ground is flat, not hilly, but gently undulating.

Both plots belong to the low alpine region (du Rietz 1950) although the vegetation of the upper, exposed parts of K2 show strong resemblance to middle alpine vegetation types.

Census methods

Throughout we have applied the territory mapping technique for the majority of the species. We followed the recommendations given by the International Bird Census Committee (see Svensson and Williamson 1969 and also Svensson 1975). For most of the species we met no particular difficulties and the density figures obtained can be considered accurate. Some species constitute exceptions, however.

For the most common species, *Anthus pratensis*, we had some difficulties in distinguishing between neighbouring territories, particularly during the first few years, when the density was very high and our experience limited. In some other species we could not use the territory mapping technique. In *Philomachus pugnax* we combined search of nests with observations of alarmed reeves immediately after hatching, but we were never quite sure that we had found all the breedings. On the contrary, over the years we have probably missed quite a few. In *Gallinago media* we based our abundance estimates on the number of males on a display ground, but since we did not count them every year during their peak display period our estimates are probably too low. Occasional visits at night in the early season indicated higher numbers. Also in *Gallinago gallinago* we had some difficulties because of their very extensive display flights. The single *Anas crecca* of 1974 was an accidental nest find and there may have been a few more breedings of this species, but not, however, of any other duck. We are certain that we have not missed any species breeding in the plots if we pool the data from all 15 years.

In order to ensure that the same principles were applied for all the years, a complete re-evaluation of all species maps were carried out in 1979. The re-evaluation produced estimates very similar to the original ones except for the first two years: In *Anthus pratensis* the original estimates were 69 and 49 pairs in K1 and 28 and 15 pairs in K2. The corresponding new estimates were 60 and 54 pairs, and 30 and 20 pairs, respectively. In the

other species and years the revised figures were not at all or only slightly shifted.

Census periods

In a multi-visit mapping census the selection of dates and hours for the visits is not as critical as when performing a single visit line transect count although care in these respects may help to increase the accuracy for low efficiency species (Svensson 1979). In spite of this we give here fairly detailed information on our visiting schedules (table 1).

The field work started as soon as the snow had melted away from most parts of the study plots. In some years most of the snow had been absent for a couple of weeks before the first visit. The time of snow-melting varies widely from year to year, but the start of the breeding season for the birds is much more constant. In all the years hatching started during the last week of June or the first week of July.

The first visit to the lower plot, K1, was paid between 11 June (1978) and 18 June (1971 and 1975). In most years the work started between 15 and 17 June. The visits were spread over a period of two to three weeks, in most years over 15-16 days. The mean date varied slightly from year to year. In 13 of the 15 years it fell within the five days period of 21-25 June, in one year (1978) on 19 June and in another year (1966) on 28 June. In 1964-1968 we made 10 visits each year and in 1969-1978 8 visits. Each visit took about 6 hrs (the annual average varied between 5 and 6.5 hrs).

In the upper plot, K2, the first visit was paid between 12 June (1978) and 24 June (1971). In most years the work started between 17 and 18 June. The visits were spread over a period of from 8 days to about 3 weeks, in most years over about 2 weeks. The mean date was most often between 24 and 29 June, but in three years earlier: 16 June (1978), 20 June (1976), and 29 June (1966). We made 5 visits each year, with the exception of 1975, when only four visits were made. Each visit took about 5 hrs (the annual mean varied between 4 and 6 hrs). In 1974 only half the plot was censused. The density figures for that year have been adjusted according to the average ratio between the two halves in the other years.

The census periods were adapted to coincide with the laying and incubation periods of the birds. The breeding synchrony between different species is pronounced and therefore all species can be accurately counted (with the provisions mentioned above) during such a brief period as 2-3 weeks or less. The reason why we made only five visits to plot K1 was of course that this plot was very easily surveyable. We compensated the lower number of visits by staying in the plot during each visit almost as many hours as in K1 in spite of the very low density in the dryer parts of the plot.

The effect of change of observers

It is known that different observers may evaluate the same species maps in different ways (Svensson 1974). By the re-evaluation of all the maps this source of error could be eliminated in our material. But different observers may also differ in the collection of field observations. Although it has been shown (Enemar et al. 1978) that the experienced observers of our team at Ammarnäs will differ only slightly when carrying out contemporary censuses in the same plot, we will here briefly consider the possibility of errors because of changes of observers between years. The observers for different years are given in table 1.

The data that we have at our disposal do not allow an assessment of the capability of each single participant, but for plot K1 we have some data that can be used. Observer SS has been working in one half of that plot in all years but one, and two other observers have been working in the other half in 5 and 7 years, respectively. For the two most common species we have calculated the ratio of the density estimates in the two halves. In 1965-1969 the mean ratio for BA/SS was 0.92 ($s=0.185$) in *A. pratensis* and 1.05 ($s=0.146$) in *C. lapponicus*. In 1970-1974 and 1976-1977 the ratio for UC/SS was 0.96 ($s=0.163$) in *A. pratensis* and 1.35 ($s=0.224$) in *C. lapponicus*. The difference between BA/SS and UC/SS was 0.04 in *A. pratensis*, which is not significant, and 0.30 in *C. lapponicus*, which is significant. Provided that there has been no change in the relative abundance of *C. lapponicus* in the two halves of the plot this might indicate a difference between BA and UC compared to SS, or a change in the efficiency of SS. The difference is small enough, however, to cause no trouble for the analysis in this paper. Other species are easier to census and a small difference in efficiency

between the different observers will hardly be possible to detect. We therefore conclude that observer differences can be neglected.

RESULTS

Taxonomic composition and number of species

Two groups of birds dominate the community, Passeriformes and Charadriidae. They are represented by about the same number of species. In plot K1 the average number of species each year was 11.1 and out of these 5.5 were passerines and 5.4 waders. In K2 the corresponding figures were 7.9, 4.3, and 3.2. As to the number of pairs, the passerines dominated over the waders in both plots. Over all the fifteen years 81.5 % were passerines, 17.9 % waders, and only 0.6 % other species.

The number of species varied somewhat from year to year. In plot K1 the number varied between 9 and 14, and in K2 between 5 and 11, giving coefficients of variation of 13 and 22 %. A total of 21 species bred at least once in K1, and 16 species in K2. In both plots together 26 species bred at least once. Thus, it is a species-poor community that we are dealing with, and, as we shall see below, only a few of these species are regular and still fewer are abundant.

Continuity of occurrence and species turnover

Only a few species occurred regularly in the study plots. In plot K1 4 passerines and 5 waders were breeding almost every year. In plot K2 there were also 4 passerines but only 3 waders that were breeding fairly regularly: two of the waders were absent in four and five of the 15 years. Combining both plots there were 5 passerines and 5 waders that bred almost every year. The bird community of our sample plots is therefore amply characterized by the following species list: *Anthus pratensis*, *Calcarius lapponicus*, *Oenanthe oenanthe*, *Phylloscopus trochilus*, *Eremophila alpestris*, *Gallinago gallinago*, *Gallinago media*, *Calidris alpina*, *Philomachus pugnax*, *Charadrius apricarius*, and *Charadrius morinellus*. The last species has been included among the regular breeders because it is possible that it was present also in years when breeding

was not established. *Luscinia suecica* is not included, although it occurred in nine years, because it is certain that it was not present in the years when it was not recorded. *Gallinago media* was not found in one of the years but it was probably present also that year.

The species turnover $T = (I + E)/(S_1 + S_2)$ (I is the number of species present in year 2 but absent in year 1, and E is the number of species present in year 1 but absent in year 2; S_1 and S_2 is the number of species in year 1 and 2, respectively) varied between years (fig. 1). Average T between two adjacent years ($n = 14$) was for K1 13.9 % (C.V. = 30.6 %), and for K2 20.1 % (C.V. = 40.2 %). The difference between the two plots is far from significant and T for both plots combined was 17.1 % (C.V. = 33.7 %). In K2 there was a rather high turnover during the last five years but otherwise there was no trend over the years.

The estimate of turnover calculated as above, using the average turnover between adjacent years, may underestimate the average long-term turnover, since one would expect adjacent years to be serially correlated. Birds that survive from one year to another tend to return to the same place, even the same territory. We have therefore calculated turnover between years further apart from each other. The result is given in fig. 2. The turnover for adjacent years is clearly below that between years further apart. In fact turnover increases to a peak for years about nine years apart. Then, interestingly, it declines again. The increase is expected, but the decline is not. Such a decline is not observed in a number of forest plots in southern Sweden (one example is given in the same figure). Might it be that there are cycles in the species composition in alpine (northern) communities? It is perhaps not purely by chance that the peak falls at about 9 years. Cycles of abundance of approximately this length are known from northern habitats. Perhaps the turnover pattern reflects environmental cycles that make the fauna of an area maximally dissimilar about every nine years? This idea deserves further analysis.

Community and population density

All the primary results on population size are given in table 2 and 3 for plot K1 and K2 separately. Since each plot was one km²

the figures directly describe the density in pairs (or territories) per km^2 . In plot K1 there were on the average 74 passerines and 17 waders and no regular species of other taxa, making together an average of 91 pairs per year. In plot K2 there were 34 passerines and 7 waders with no other regular species either. The total density thus was about half that of K1 or 41 pairs. The lower density of K2 was mainly due to the fact that half that plot lay on a dry ridge with vegetation similar to that of the middle alpine region. The two plots combined represent fairly well the two dominating habitats in the low alpine region of the area (heaths and bogs) and the density estimates obtained should roughly characterize large areas of the Ammarnäs region. The average density of birds, including both rich and poor habitats, should then be about 60-70 pairs/ km^2 . To this should be added only that neither plot contained any lakes, ponds or larger streams. Some alpine areas in the region include such components but it is probable that the overall density would increase only slightly if this is taken into consideration.

In plot K2 about half of the plot was covered with vegetation more similar to that of K1 than the rest (see above). If we consider the two halves separately we find that the lower and richer half carried 62 pairs/ km^2 (52 passerines, 9 waders) but the upper half only 20 pairs/ km^2 (15 passerines and 5 waders). Thus the density of the lower half is more similar to that of K1. It was 61 % of that of K1 whereas the density of the upper half was only 22 % of that of K1.

In both plots *Anthus pratensis* was the commonest species with 38 and 15 pairs per year. *Calcarius lapponicus* was the second most common with 22 and 10 pairs. The third species was different in K1 and K2. In K1 *Phylloscopus trochilus* took this position with 7 pairs and in K2 *Oenanthe oenanthe* took it with 6 pairs. These most abundant species were all passerines and they constituted together c. 75 % of all birds.

Population and community structure fluctuations

The population fluctuations are given by the coefficients of variation (C.V.) in table 2 and 3. The coefficients are slightly higher in K2 than in K1 for comparable densities. In K1 there are two species that differ drastically from the rest: *Luscinia suecica* and *Phylloscopus trochilus*. Both these species belong to

the category of woodland birds that periferically extend the range up into the lower parts of the alpine region. The violent fluctuations probably reflects the fact that the alpine habitats are suboptimal for these species. The fluctuations may be caused by a particularly variable resource in the alpine habitats or, more probably, reflect events in the subalpine birch wood (spill-over from an optimal habitat).

The fluctuations in K1 and K2 seems to be fairly normal for alpine habitats. The few multi-year studies that are available provide similar coefficients of variation. Moksnes (1973) obtained a C.V. of 22 % for *A. pratensis* and 11 % for the whole community, and the Finse data (Stenseth 1979) gave a C.V. of 32 % for *A. pratensis*.

The variation for some community structure variables are given in fig. 3.. Total abundance has a slight downward trend but this is caused exclusively by *A. pratensis*. The rest of the community shows an increasing trend. Also the number of species has increased but the trend is far from significant. Diversity, the Shannon's H' , has increased over the years. For both plots together there is a rather small variation around the trend line, but much higher in K2 alone. Eveness, e , shows the same pattern. Thus, over the 15 years the community has become slightly more rich in species, the common species has become less common, and the diversity and eveness has increased.

DISCUSSION

Representativity of the study plots

The question of the representativity of the study plots in relation to the population dynamics of the whole Ammarnäs area will be dealt with in detail in a forthcoming paper. Here we will only compare the species composition of the study plots with that of the Ammarnäs region in general. A summary is presented in table 4.

The species have been divided into three categories based on their habitat preferences. The birds of category A, mainly woodland species, are represented in the lower plot, K1, by *Phylloscopus trochilus* in most years, and by *Luscinia svecica* and *Turdus iliacus* in about half the years. Some other species occur occationally. The birds of category B, mainly bog and grass-

land species of both alpine, subalpine and boreal distribution, are well represented. Six species, *Gallinago gallinago*, *Gallinago media*, *Calidris alpina*, *Philomachus pugnax*, *Oenanthe oenanthe*, and *Anthus pratensis*, bred in at least one of the plots in most years. A few more species of this category occurred occasionally. The birds of category C, the true alpine species, were represented by four species regularly: *Charadrius apricarius*, *Charadrius morinellus*, *Eremophila alpestris* and *Calcarius lapponicus*.

The reason why some of the other regularly breeding species of the region did not appear regularly in the plots was that their overall density is very low or that there are no suitable habitat or nestsite within the plots. Some of these species were observed as visitors more or less regularly in the plots. In some species the population density in the whole Ammarnäs region varies drastically from year to year, for example in *Carduelis flammea* and *Stercorarius longicaudus*, this being the main reason for their irregular occurrence.

Thus, the percentage of the species breeding in alpine habitats in the Ammarnäs region, represented regularly in the study plots were for the three categories A, B, and C: 33 %, 40 %, and 44 %, respectively, giving a percentage of 38 for all species together. Therefore, it seems safe to conclude that the birds breeding in the study plots constitute a fair sample of those occurring in alpine habitats in this part of Sweden. Furthermore, with only four exceptions, none of the species that did not breed regularly within the plots, occur anywhere else in the alpine parts of the Ammarnäs region dense enough to be sampled adequately with plots of two km². The four exceptions are *Charadrius hiaticula*, *Calidris temminckii*, *Calidris maritima*, and *Plectrophenax nivalis*, which locally may breed with fair numbers in relatively small areas.

Co-variation between the two study plots

The two study plots are, as mentioned earlier, located very close to each other; the distance between the closest parts is only about 1 km. One would therefore expect to find the same density changes between the years in both plots.

The correlation coefficients for the three most abundant passerines common to both plots were: +0.70 (*Anthus pratensis*), +0.01 (*Calcarius lapponicus*), and +0.12 (*Oenanthe oenanthe*). In

Charadrius apricarius, the only regular wader common to both plots, we found a correlation coefficient of -0.34 . All waders pooled produced a coefficient of $+0.22$. Only the coefficient for *Anthus pratensis* is significantly different from zero.

With the exception of *A. pratensis* and *C. lapponicus* it is not surprising that we did not obtain significant correlation coefficients: the sample sizes were very small. It is surprising, however, that there is no correlation at all between the two plots for *C. lapponicus* although it is for *A. pratensis*. We have no explanation to this difference between the two dominating species. It can be observed that in 1974 the number of *C. lapponicus* was higher in K2 than in K1 and remarkably higher than in any other year in K2. Neither for this unexpected peak we can find any explanation. In some areas one finds concentrations of many pairs of *C. lapponicus*, almost loose colonies, but we have not observed this in our study plots. So, shifts of colony location cannot explain the 1974 peak in K2.

The conclusion we must draw is that it is not always safe to make general inferences about population fluctuations from small samples, neither to base a community description on census data from only one or two years. This question of how widespread population changes are will be further elaborated below.

Co-variation between different species

Correlation coefficients were calculated for each of the three pairwise combinations of the three most abundant species in each of the two study plots. They were in plot K1: -0.24 for *C. lapponicus*/*P. trochilus*, $+0.15$ for *A. pratensis*/*P. trochilus*, and -0.30 for *A. pratensis*/*C. lapponicus*. None of them differed significantly from zero. In plot K2 they were: $+0.39$ for *C. lapponicus*/*Oe. oenanthe*, $+0.60$ for *A. pratensis*/*Oe. oenanthe*, and $+0.27$ for *A. pratensis*/*C. lapponicus*. Only the coefficient for *A. pratensis* versus *Oe. oenanthe* was significantly different from zero.

There was no correlation between *P. trochilus* and *L. suecica*, which might have been expected if there were some common factor governing the occurrence of these two woodland species in the alpine habitats. The factors that determine the occurrence of these species above the forest line are therefore probably independent.

One might draw one conclusion from the fact that we obtained three positive correlation coefficients in K2 (although only one

of them significant) but two negative and only one positive in K1: Some local factors may be operating with heavier effects in K2 than in K1. The most probable factors are adverse weather conditions: later snow-melting and higher exposure to cold spells late in the season.

The structure and diversity

The species abundance structure of the community is fully described by the dominance curves with the species in their abundance sequence. Several different theoretical models can be tested against the observed structure. Commonly used are the broken-stick model, the log-normal model, and the geometric series model (roughly equivalent to the log-series model). The broken-stick model has been discussed by MacArthur (1957, 1960) and by Whittaker (1972). This is the structure to be expected in a community if the species are partitioning some major resource randomly among themselves. It is a distribution that is more even than the log-normal one. The log-normal distribution is a kind of universal outcome if there are many factors, many different resources, that affect the community and for which the species compete. As soon as there are many species this distribution is to be expected as a result of purely statistical reasons, i.e. a result of the central limit theorem that says that several distributions when added will asymptotically approach normality. The geometric series distribution describes a situation when the species of a relatively simple community are governed by a dominating environmental factor, pre-empting in some sequence the same fraction of what is left of the resources by the species already established. If, for example, as argued by Boswell and Patil (1971) a log-series distribution, superficially similar to a geometric series distribution, is expected when species arrive in an area at uniform but random time intervals, each species as it arrives occupying a certain fraction of the resources that remain: it is the 'free-for-all' situation.

Several authors have compared and contrasted the different models (Pielou 1969, May 1975). May provides a brief summary stressing the fact that the lognormal distribution is not a result of biological constraints on a community, whereas the other two distributions are. The broken stick model is the result of random effects if the intrinsic distribution is even and the

geometric (or log) series model is the result of the uneven nich-preemption property of the community, both reflecting different, biologically meaningful constraints on species abundances. Whittaker (1965) found that dominance curves approximating a geometric series were common especially in pioneer and ephemeral communities and in those which have rigorous environments and relatively few species.

In fig. 4 we have compared the species abundances (expressed as percent dominance) found in the Ammarnäs plots K1 and K2 with the different theoretical distributions. It can be seen that the best fit is obtained with a straight line in the log-lin diagram which is a property of the geometric series. Both the broken stick and the lognormal distribution give a less good fit. It is only the two most abundant species that are too abundant to fit the geometric series well. It should be remarked that the regression line is the line fitted to the log-dominance values. Therefore the area under the line is not 100 % as it is for the other two curves. The overabundance of the two commonest species may indicate a tendency towards the lognormal distribution, but as shown below this overabundance disappears when biomass instead of numbers are used for calculation of species importances.

But in any case, the geometric series provides the best fit out of the three model distributions tested. Therefore we have used this model for the comparisons to follow. In fig. 5 we have compared the two plots K1 and K2 and it can be seen that in K2 also the most abundant species fall on the line. This is in agreement with the theory since the community of K2 is simpler than that of K1 and more dominated by fewer environmental factors. We have also compared the two dominating taxa of the plots, the passerines and the waders (fig. 6). The passerine part of the communities fits very well to the geometric series distribution while the wader part gives a less good fit in plot K1 (the fit in K2 is extremely good also for the waders).

There is a still better fit to a geometric series distribution when the dominance values are based on biomass rather than on numbers (fig. 5). This indicate that the apparent overabundance of the two most common species is caused by their small size (*Anthus pratensis* and *Calcarius lapponicus*) and their lesser share of the total energy flow through the birds than is indicated by abundance importance.

In summary it can be concluded that the resources channeled through the birds in the alpine region of the Ammarnäs area are partitioned among the species according to a geometric series distribution. As a consequence of this one should expect some dominating environmental factor to be operating. A good guess seems to be the adverse climatic conditions giving a small and poorly diversified energy base for the bird community. Also, the alpine habitats could be considered to be a kind of pioneer community, permanently forced into the pioneer state by these adverse conditions.

Species versus time relationships

An average of 14 species bred each year but 26 species bred at least once during the 15 years of census in the two plots. It is reasonable to assume that more species will be added to the list in the future. How fast will they be added?

The increase in the number of species with the number of years included in the census period follows very closely a straight line in a log-log diagram for K1 and K2 pooled. The slope of the line is just above 0.24, and the regression equation consequently

$$\ln S(t) = 0.24 \ln t + \ln 14$$

where $S(t)$ is the number of species found during t years, and 14 the average number of species in a single year. The slope is almost exactly the one expected from Preston's (1962) canonical hypothesis for species-area relations.

If the sample plots are representative of a much larger area and if the birds redistribute randomly within that larger area each year the time dimension can be exchanged freely with the area (or community abundance) dimension. Fifteen years of census in the plots should then correspond to a census of 30 km^2 and the successive years with a stepwise increase of the area with 2 km^2 .

If we extrapolate the species/time line into the future we will find that about 45 species will be found breeding in the plots during the next 130 years (a brief episode in the long-term undertakements of the Luvre research team). This particular combination of species number and years was selected since 45 species is the approximate maximum number of species that will possibly be able to breed in the habitat in question. Since there is a maximum number of species that can breed (it will always be if evolutionary time perspectives are neglected) the line is not

really a straight line: the rate of increase in number of species will decline and the time when all 45 species have been found breeding will be in a more distant future than 130 years.

We know the breeding bird fauna of the mountains surrounding K1 and K2 well enough to estimate very accurately the number of species that we could expect to breed in an average year in an area of 30 km^2 (15 times the census plots). This figure is very close to the 26 species we have found during the 15 years of census within the plots. A further increase of the area would add very few species in an average year. Even with an increase of the area corresponding to 130 years (260 km^2) would give a species list below 30, thus far from the 45 potential species.

It is easy to see why we have this discrepancy between the number of species found in an area A during T years versus the number found in an area TA during one year: the temporal variation in the appearance of rare species is more violent than spacial variation in species occurrences in any one year. And this, in turn, is caused by the fact that some species do not breed at all in the alpine habitats of the region in some years, and particularly because some species will occur extremely rarely.

We can now quantify species number increases along the space and time dimensions. The number of species observed in plots of the approximate size used in our work will double over a period of 15-20 years. About the same increase will be obtained by increasing the plot size 15-20 times. Over such a comparatively brief period of time there will probably be no great difference between time and space increases, but for longer periods of time the increase in species numbers will be steeper along the time dimension than with increasing area.

Since we can expect roughly the same number of species within a plot 15-20 times larger than ours as after 15-20 years in these plots the species-area relation, i.e. the slope of the species area curve would be around 0.25. Thus there is no island effect involved, and none was expected.

Comparison with other censuses in similar habitats

Northern bird communities in alpine or similar habitats have been censused to some extent. In Scandinavia there are three studies of alpine or subalpine bog/heath areas roughly similar to those of our study (We are considering only studies in which multi-

visit mapping counts have been applied). Moksnes (1973) studied three subalpine plots (c. 0.5 km^2 , c. 800 m a.s.l.) and one alpine plot (0.28 km^2 , 840-1400 m a.s.l.) in 1967-1971 in the Nedal area of Norway (63°N). Lien et al. (1974) reported censuses from four plots near Finse (c. 60°N), also in Norway. The plots covered together c. 1 km^2 and were censused 3-6 years in the period 1967-1972. The elevation was from 1200 to about 1500 m a.s.l. Moksnes (1971, 1972) also studied an area at a lower elevation, a bog area at Foradal in Norway (c. 64°N). The elevation was 400-440 m with the forest line at 500-550 m. Two plots varying a little in size between years ($0.5\text{-}1 \text{ km}^2$) were censused in 1970-71.

For comparative purposes I have also included a study of three bogs (together 1.1 km^2) in southern Sweden at 60°N (Svensson 1978).

Some other relevant studies refer to Skokholm island (Lockley 1935), NW Iceland (Glue 1970), and W Greenland (Longstaff 1932). We have also included in the comparison four areas on tundra in Alaska: Point Barrow and Prudhoe Bay (Norton et al 19) and Cape Krusenstern and Cape Prince of Wales (VanVelzen 1977).

Summarized data from these censuses are found in table 5. All the communities are poor in species. With the exception of the Iceland plot (much larger than the other) a maximum of 14 species bred in an average year. The number of passerines shows a maximum of seven. It is difficult to compare the number of species, however, since plot size varies. Some of the most important differences in other respects deserve mentioning. It is particularly the Alaskan plots that differ from the other. Three of them have more waders than passerines whereas in all but one of the other plots there are more passerines than waders.

The densities vary considerably. It is low in the Greenland and Iceland plots. These are very large and comprise different kinds of habitats, some of which support very few birds. In the West Greenland plot about 20 % of the area was water, for example. Otherwise it seems that the tundra plots in Alaska are richer than the Scandinavian heath/bog plots. Much depends, however, on the selection of the sample sites. The Ammarnäs plots were not selected because the bird fauna was particularly rich, but because we expected it to be 'average'. In spite of this we have found densities in K1 in some years that approaches those found in the Alaskan tundra plots. One should therefore probably not give too much weight to the density differences. On the other hand,

the differences in species composition is probably a real difference between the coastal tundra and alpine and subalpine bog/heath areas. Unpublished reports from tundras in arctic USSR provide indications of the same kind: a predominance of waders over passerines.

The boreal mire at Finse also had more waders than passerines but the opposite relation was found on the boreal mires at Grimsö. It is obvious that too few censuses are available for generalizations.

There are also a number of line transects made in alpine and similar heath/bog habitats, particularly in northern Scandinavia (e.g. Granit 1938 and Bagge et al. 1963). Recently Järvinen and Väisänen (1978) presented extensive line transect data from northern Norway (230 km), covering a number of different alpine and coastal heaths and bogs. Their data were collected by single visits to the different habitats, with the visits spread over about one month. Further, they assumed that all species were censused with the same efficiency within their transect strips 50 m broad. According to our experience at Ammarnäs the census efficiency of many species differ widely over such an extended period as one month, and we have also found that the census efficiency of different species are far from equal. We have already described the difficulties and the low efficiency in some waders. The same problem when censusing waders was stressed by Meltofte (1976, 1979). He said that it was essential to survey the plot many times during the breeding season to obtain accurate figures for waders. As a consequence of this we wish to show some care in comparing uncorrected line transect data with data from multi-visit mapping studies, and we therefore refrain from doing that presently.

How widespread are the population changes?

There are several different kinds of data that can be used for determining whether changes in an area are local or represent a widespread pattern: breeding bird censuses from scattered areas, ringing totals and migration counts. The latter measures will integrate population changes over vast areas. But they are difficult to use since they are sensitive to weather conditions during migration (Edelstam 1972, Svensson 1978). However, if results

from many years are available one would still expect some correlation with breeding bird censuses.

There is one species among those censused at Ammarnäs for which such a comparison can be carried out: *Anthus pratensis*. It has been counted in fairly high numbers at three localities along the Scandinavian mountains: Ammarnäs, Nedal (Moksnes 1973), and Finse (Stenseth 1979). Ringing totals are available from Sweden and Norway and migration totals have been collected at Falsterbo in 1973-1978. The data are given in fig. 7.

There is a good agreement between Ammarnäs and Nedal but not between Ammarnäs and Finse. There is also a good agreement between Ammarnäs and the ringing totals for Sweden, and a similar agreement is found between Finse and the ringing totals for Norway. In the latter case two peaks coincide precisely. The correlation between Ammarnäs and the Swedish ringing totals is also shown in fig. 8, where it can be seen that the correlation is about 0.79, which is significantly different from zero.

It is surprising that the agreement between census data from small remote areas and ringing totals for whole countries is so good. It is difficult, however, to tell why there is a weaker correlation between Finse and Ammarnäs and between the Swedish and Norwegian ringing totals. We may be dealing with two different populations with different wintering areas, but the recoveries that we have studied do not provide any clear support for this idea.

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Table 1. Specification of census data in plots K1 and K2.

Year	Plot K 1					Plot K 2				
	No of visits	Date of 1st visit (June)	Census period (days)	Mean hrs/visit	Census date	Census takers ²	No of visits	Date of 1st visit (June)	Census period (days)	Mean hrs/visit
1964	10	15	16	9.0	22	A, E, Ha, M, S	5			A, E, Ha, M, S
1965	10	16	15	11.5	22	A, S	5	23	13	29
1966	9	17	21	9.0	28	A, S	5	17	23	22
1967	10	12	27	10.0	23	A, S	5			
1968	10	15	17	8.2	22	A, S	5			
1969	8	13	21	6.1	22	A, S	5	18	20	28
1970	8	16	15	6.3	23	C, S	5	20	12	26
1971	8	18	15	4.9	25	C, S	5	24	9	29
1972	8	15	16	5.0	23	C, S	5	21	11	26
1973	8	17	18	5.3	25	C, S	5	22	17	28
1974	8	17	14	6.1	23	C, S	5	18	15	25
1975	8	18	16	5.6	25	H, S	4	18	15	24
1976	8	14	14	6.0	21	C, S	5	17	12	20
1977	8	17	15	6.0	25	C, L, S	5	18	15	26
1978	8	11	19	6.6	19	C, L	5	12	8	16

¹Only half K 2 censused, hrs given is twice the time used in half plot.

²A=Bengt Alm, C=Ulf T. Carlsson, E=Anders Enemar, Ha=Sven Åke Hanson, H=Lars Hellsborn, L=Göran Liljedahl, M=Harry Myhrberg, N=Erik Nyholm, S=Sören Svensson

Table 2. Number of permanent territories or breeding pairs in the low elevation alpine plot K 1 in 1964 - 1978. Each plot covers 1 km², so the figures directly give the densities in pairs/km².

Species	1964	65	66	67	68	69	70	71	72	73	74	75	76	77	78	Mean	c.v. %	Year
<i>Anthus pratensis</i>	60	54	56	48	38	40	35	24	24	31	34	33	27	32	33	37.9	30.2	15
<i>Calcarius lapponicus</i>	15	15	29	26	23	19	20	25	24	20	22	24	22	24	23	22.1	17.3	15
<i>Phylloscopus trochilus</i>	10	4	10	2	0	20	15	5	4	2	10	4	7	7	8	7.2	73.3	14
<i>Oenanthe oenanthe</i>	3	3	3	2	2	4	2	3	2	1	2	2	2	2	5	2.5	39.1	15
<i>Luscinia suecica</i>	7	4	2	0	0	0	0	0	1	1	5	7	6	0	2	2.3	116.4	9
<i>Turdus iliacus</i>	0	0	0	0	0	2	0	0	0	0	3	2	1	2	1			6
<i>Carduelis flammea</i>	0	0	0	0	2	0	0	2	0	0	0	1	0	0	0			3
<i>Emberiza schoeniclus</i>	0	0	0	0	0	0	0	0	1	0	1	0	0	0	2			3
<i>Turdus pilaris</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0			2
<i>Anthus cervinus</i>	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0			1
<i>Gallinago gallinago</i>	3	6	6	7	3	5	4	7	5	5	7	5	5	4	5	5.2	27.4	15
<i>Calidris alpina</i>	3	1	2	5	3	5	2	3	4	3	5	3	4	3	4	3.3	35.3	15
<i>Philomachus pugnax</i>	2	4	2	5	3	3	2	2	2	2	5	4	4	4	3	3.1	35.9	15
<i>Pluvialis apricaria</i>	3	2	2	1	2	2	3	4	2	3	2	4	2	3	5	2.7	39.2	15
<i>Gallinago media</i>	2	0	3	3	3	3	2	2	1	2	2	1	3	2	3	2.1	42.9	14
<i>Tringa glareola</i>	3	1	0	0	1	1	0	0	1	0	0	0	0	0	0			5
<i>Calidris temminckii</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0			1
<i>Charadrius morinellus</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0			1
<i>Stercorarius longicaudus</i>	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1			2
<i>Lagopus lagopus</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0			1
<i>Anas crecca</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0			1
Passerines, total	95	80	100	78	65	86	72	59	56	55	77	73	67	68	74	73.7	17.8	
Charadriidae, total	16	15	16	21	15	19	13	18	15	15	21	17	18	16	20	17.0	14.2	
Other species	0	0	0	0	0	0	0	0	0	0	3	1	0	0	1	0.3		
Total no. of pairs	111	95	116	99	80	105	85	77	71	70	101	91	85	84	95	91.0	15.2	
No. of species, passerines	5	5	5	4	4	6	4	5	6	5	7	7	7	6	7	5.5	20.3	
No. of species, waders	6	6	6	5	6	6	5	5	6	5	5	5	5	5	5	5.4	9.4	
No. of species, all	11	11	11	9	10	12	9	10	12	10	14	13	12	11	13	11.1	12.6	

Table 3. Number of permanent territories or breeding pairs in the high elevation alpine plot K 2 in 1964 - 1978. The plot covers 1 km², so the figures directly give the densities in pairs/km².

Species	1964	65	66	67	68	69	70	71	72	73	74	75	76	77	78	Mean	C.V. %
<u>Anthus pratensis</u>	30	20	20	18	4	20	19	10	11	14	23	12	7	8	9	15.0	47.5
<u>Calcarius lapponicus</u>	10	2	4	7	2	7	14	11	12	9	28	11	9	10	7	9.5	64.9
<u>Oenanthe oenanthe</u>	13	4	7	5	2	6	5	4	4	9	10	5	8	4	8	6.3	46.1
<u>Eremophila alpestris</u>	1	2	3	4	2	2	2	3	2	2	4	2	3	0	1	2.2	49.2
<u>Plectrophenax nivalis</u>	0	0	0	0	0	0	2	1	0	0	10	0	1	0	0		4
<u>Turdus pilaris</u>	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0		2
<u>Pluvialis apricaria</u>	4	2	3	4	2	3	3	3	4	3	6	3	3	2	2	3.1	33.8
<u>Charadrius morinellus</u>	2	0	2	3	0	0	2	2	2	3	3	0	2	2	1	1.6	70.1
<u>Calidris alpina</u>	0	1	1	2	0	1	1	0	1	2	0	0	2	1	1	0.9	85.8
<u>Gallinago gallinago</u>	0	0	0	0	0	0	0	0	2	2	2	0	0	1	1		5
<u>Calidris temminckii</u>	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0		4
<u>Charadrius hiaticula</u>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0		1
<u>Calidris maritima</u>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0		1
<u>Philomachus pugnax</u>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0		1
<u>Cuculus canorus</u>	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0		2
<u>Stercorarius longicaudus</u>	0	0	0	1	0	0	2	0	1	1	0	0	0	0	0		4
Passerines, total	54	28	34	34	10	35	42	29	29	35	75	30	28	23	25	34.1	43.4
Charadriidae, total	7	5	7	9	2	4	6	5	9	10	11	3	9	7	5	6.6	40.0
Other species	0	0	0	1	0	0	2	0	1	1	0	0	1	1	0	0.5	
Total no. of pairs	61	33	41	44	12	39	50	34	39	46	86	33	38	31	30	41.1	40.0
No. of species, passerines	4	4	4	4	4	4	5	5	4	5	5	4	5	4	4	4.3	11.3
No. of species, waders	3	4	4	3	1	2	3	2	4	4	3	1	5	5	4	3.2	39.5
No. of species, all	7	8	8	8	5	6	9	7	9	10	8	5	11	10	8	7.9	22.1

Table 4. General description of the breeding bird fauna of the lower and middle alpine regions of the Ammarnäs area, with comparison with the bird fauna in the study plots (waterfowl and gulls excluded).
 Explanations: L = low alpine region, M = middle alpine region, x = regular breeder, (x) = occasional breeder, o = no suitable nest site within the plots, + = observed but has not bred in the plot. The figures for K1 and K2 denote the number of years that each species has bred.

Category and species	Region		No. of years	
	L	M	K1	K2
Category A: Birds belonging to areas below the forest line and more or less regularly extending their ranges into the lower parts of the low alpine region (mainly woodland birds).				
Lagopus lagopus	x	-	1	0
Tringa glareola	x	-	5	0
Asio flammeus	(x)	-	0+	0
Alauda arvensis	(x)	-	0+	0+
Motacilla flava	x	-	0+	0
Saxicola rubetra	(x)	-	0+	0
Turdus pilaris	x	-	2	2
Turdus iliacus	x	-	6	0+
Turdus torquatus	x	- o	0	0
Luscinia svecica	x	-	9	0+
Phylloscopus trochilus	x	-	14	0+
Carduelis flammea	x	-	3	0+
Emberiza schoeniclus	x	-	3	0+
Category B: Birds belonging both to alpine areas and areas below the forest line (mainly birds of open lands: bogs, grasslands, etc.).				
Aquila chrysaetos	x	x o	0+	0+
Buteo lagopus	x	x o	0+	0+
Falco rusticolus	x	x o	0	0
Charadrius hiaticula	x	x	0+	1
Gallinago gallinago	x	x	15	5
Gallinago media	x	-	14	0
Tringa totanus	x	-	0+	0+
Tringa hypoleucos	x	- o	0	0
Phalaropus lobatus	x	- o	0+	0
Calidris temminckii	x	x	1	4
Calidris alpina	x	-	15	10
Philomachus pugnax	x	-	15	1
Cuculus canorus	x	x	0+	2
Oenanthe oenanthe	x	x	15	15
Anthus pratensis	x	x	15	15
Anthus cervinus	(x)	-	1	0
Corvus corax	x	x o	0+	0+
Category C: Birds belonging to alpine habitats exclusively (may extend the range below tree line but rarely below forest line).				
Lagopus mutus	x	x	0	0+
Charadrius apricarius	x	x	15	15
Charadrius morinellus	x	x	1	11
Calidris maritima	x	x	0	1
Stercorarius longicaudus	x	x	2	4
Nyctea scandiaca	(x)	(x)	0+	0
Eremophila alpestris	x	x	0	14
Calcarius lapponicus	x	x	15	15
Plectrophenax nivalis	x	x	0	4

Table 5. Comparison of species richness, densities and dominances in different areas.

Ap=Anthus pratensis, Cl=Calcarius lapponicus, Oe=Oenanthe oenanthe, Ch=Charadrius apricarius, Cf=Carduelis flammea, Pn=Plectrophenax nivalis, Tt=Tringa totanus, Aa=Alauda arvensis, Hh=Haematopus haematopus, Ca=Calidris alpina, Pf=Phalaropus fulicarius, Cm=Calidris melanotos, Cp=Calidris pusilla, Ps=Passerculus sandwichensis, Em=Eurenetes mauri, Pl=Phalaropus lobatus.

Area:	Ammaqnäs	Finse	Nedal	Foradal	Grimsö	Skokholm	Barrow	Prudhoe	Krusenst.	P	Wales	Iceland	Greenl.
Size km ² :	2.0	c. 1.0	c. 0.5	c. 0.7	1.1	0.9	0.6	0.8	0.3	0.25	5.1	20	
Yrs of study:	15	6	5	2	1	7	2	2	1	1	1	1	
No. of species													
Passerines	7	5	4	4	4	7	2	1	3	1	6	5	
Waders	6	4	4	7	5	2	8	6	7	5	7	2	
Waterfowl	0	0	0	1	0	0	2	0	2	2	5	5	
Others	1	0	2	1	1	2	0	0	1	0	2	2	
Total	14	9	10	13	10	11	12	7	13	8	20	14	
Density (pairs per km ²)													
Passerines	54	54	65	27	31	74	36	8	79	8	11	31	
Waders	12	8	20	36	11	45	89	89	47	100	6	2	
Others	+	+	5	2	1	2	13	0	7	8	3	3	
Total	66	62	90	65	43	121	138	97	133	116	20	36	
Dominance %													
Passerines	82	86	73	41	71	61	26	9	60	7	55	85	
Waders	18	13	22	54	25	37	64	91	35	86	29	6	
Others	+	1	5	4	4	2	10	0	5	7	16	9	
Dominant species %													
Ap 40	Ap 41	Ap 61	Ap 26	Aa 31	Ap 38	Cp 41	Ps 33	Em 59	Ap 36	Cl 44			
Cl 24	Oe 22	Ch 15	Ch 14	Ap 29	Hh 29	Pf 31	Ca 16	Ca 17	Ch 10	Cf 20			
Oe 7	Cl 9	Oe 5	Tt 13	Ch 10	Oe 15	Cl 8	Cm 14	Cl 7	Pf 13	Pn 12			
3 commonest %	71	72	81	53	70	82	53	80	68	83	53	76	

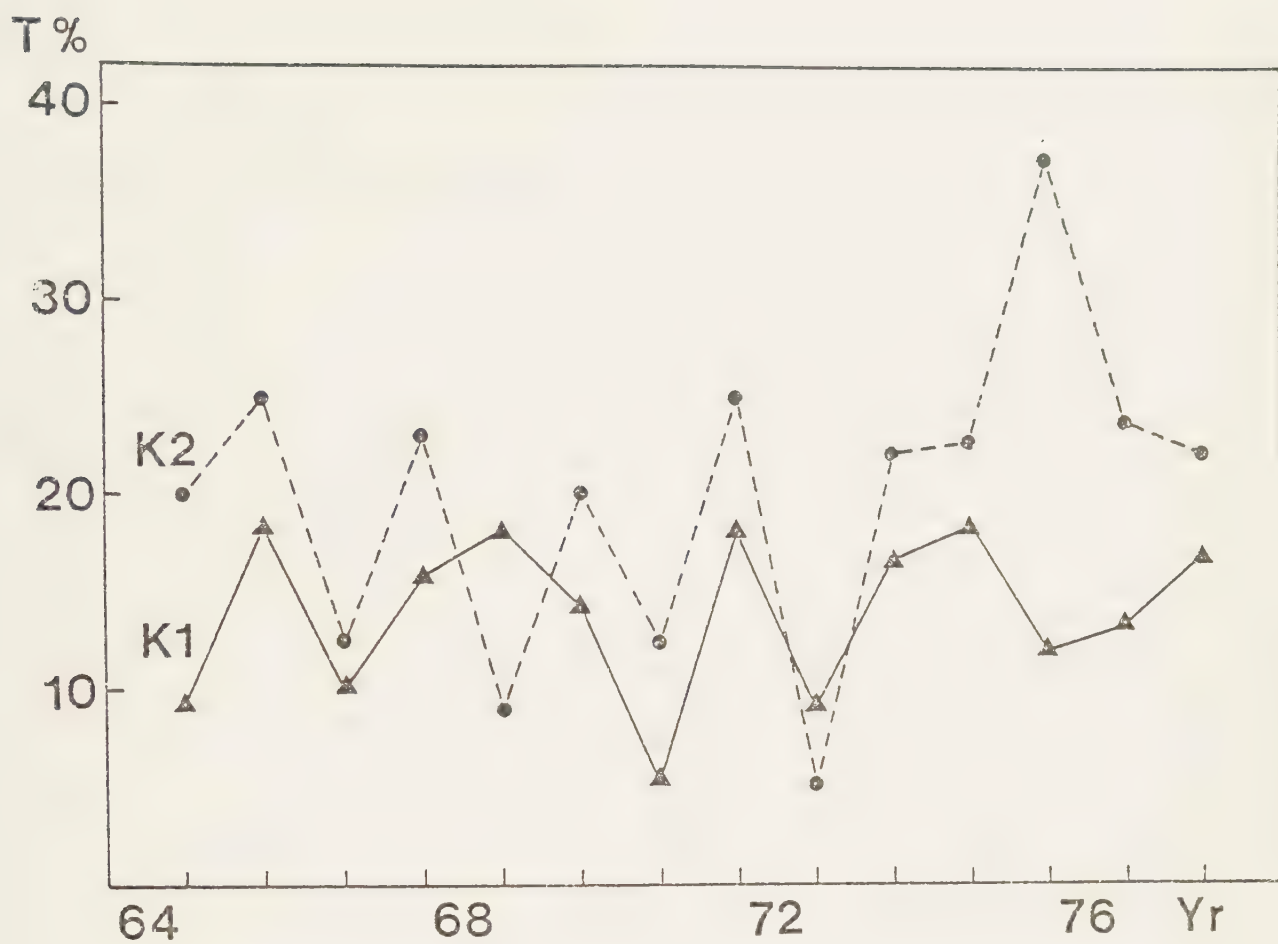


Fig. 1. Species turnover between adjacent years in K1 and K2.

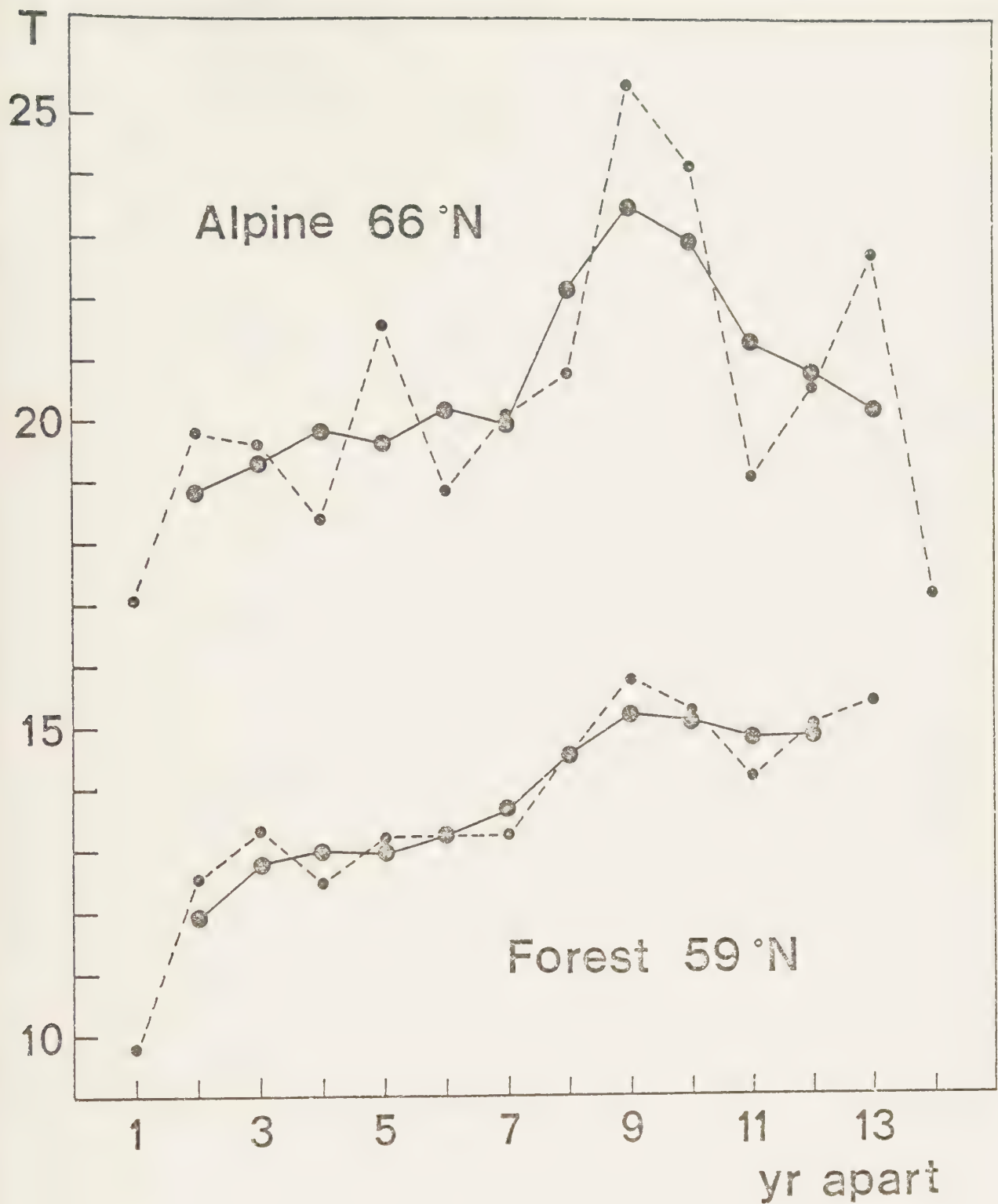


Fig. 2. Species turnover between years different number of years apart. Upper curve = K1 and K2 at Ammarnäs. Lower curve = a forest habitat in south Sweden. Larger dots = running mean over three years.

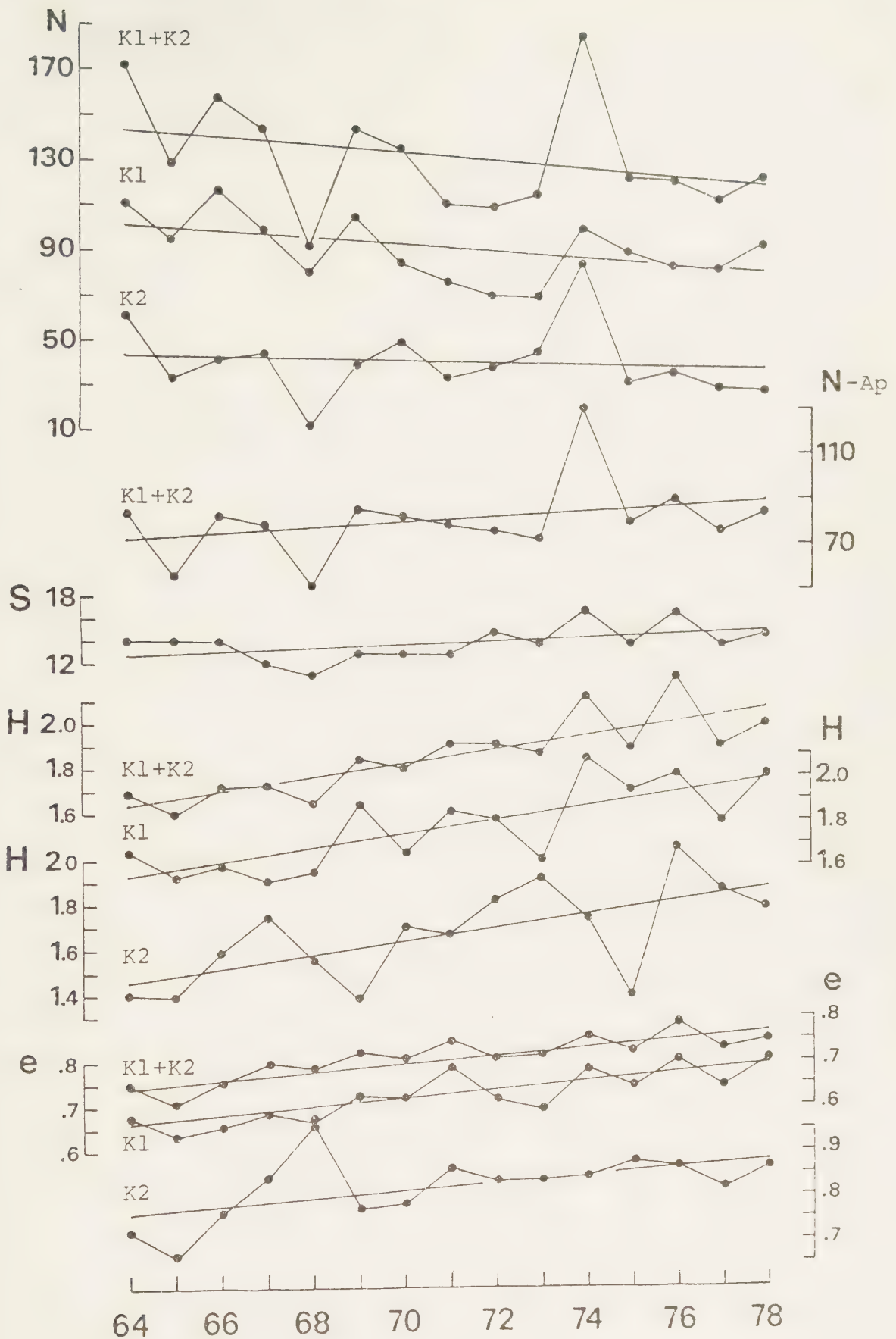


Fig. 3. Fluctuations of some community structure indices. N = No. of pairs. N-Ap = The same with *A. pratensis* excluded. S = No. of species. H = Shannon diversity. e = evenness.

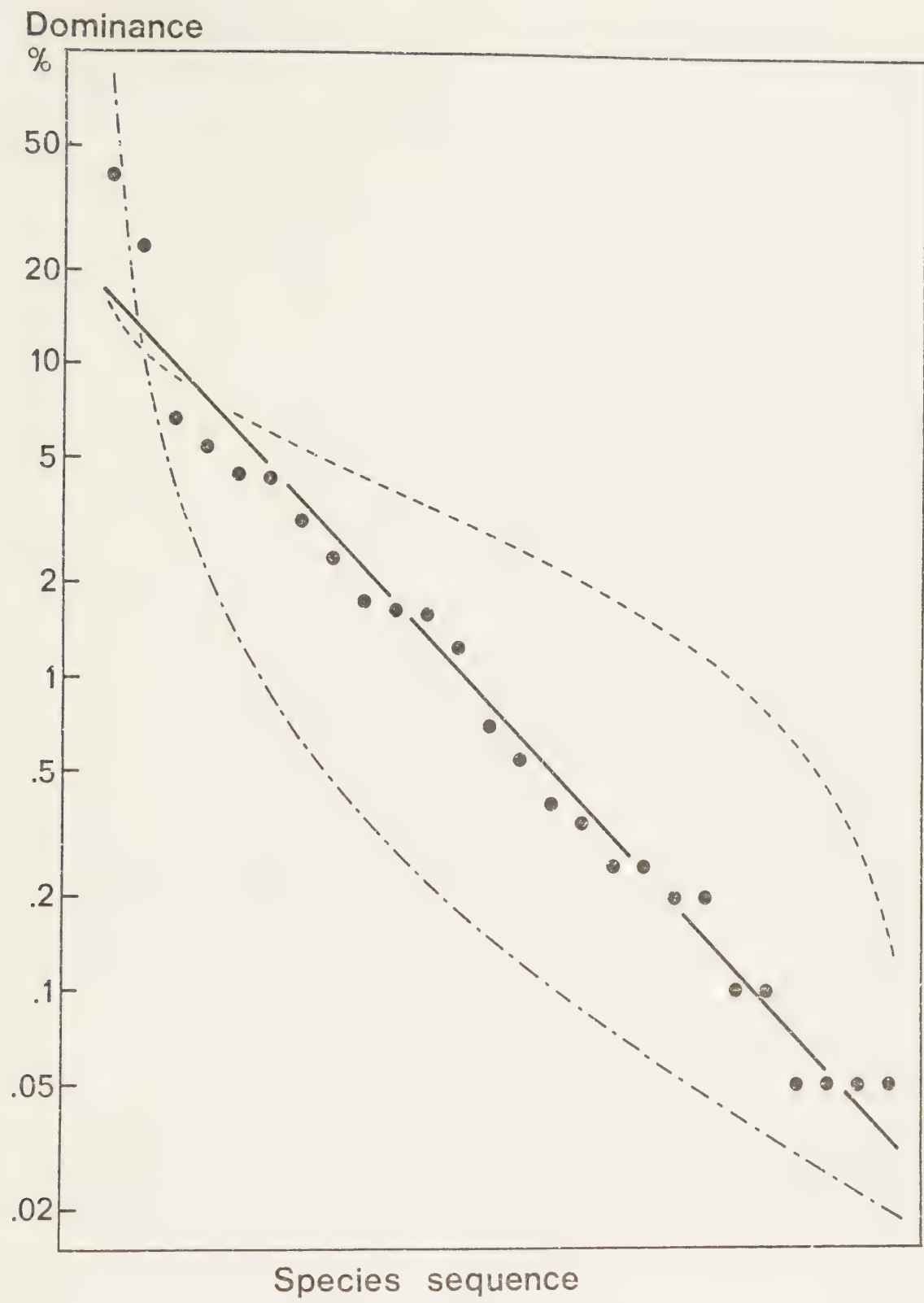


Fig. 4. Species dominance curves for the birds in K1 and K2 at Ammarnäs (dots) with the fitted regression line. The other two curves are the broken-stick distribution (upper) and the log-normal distribution (lower).

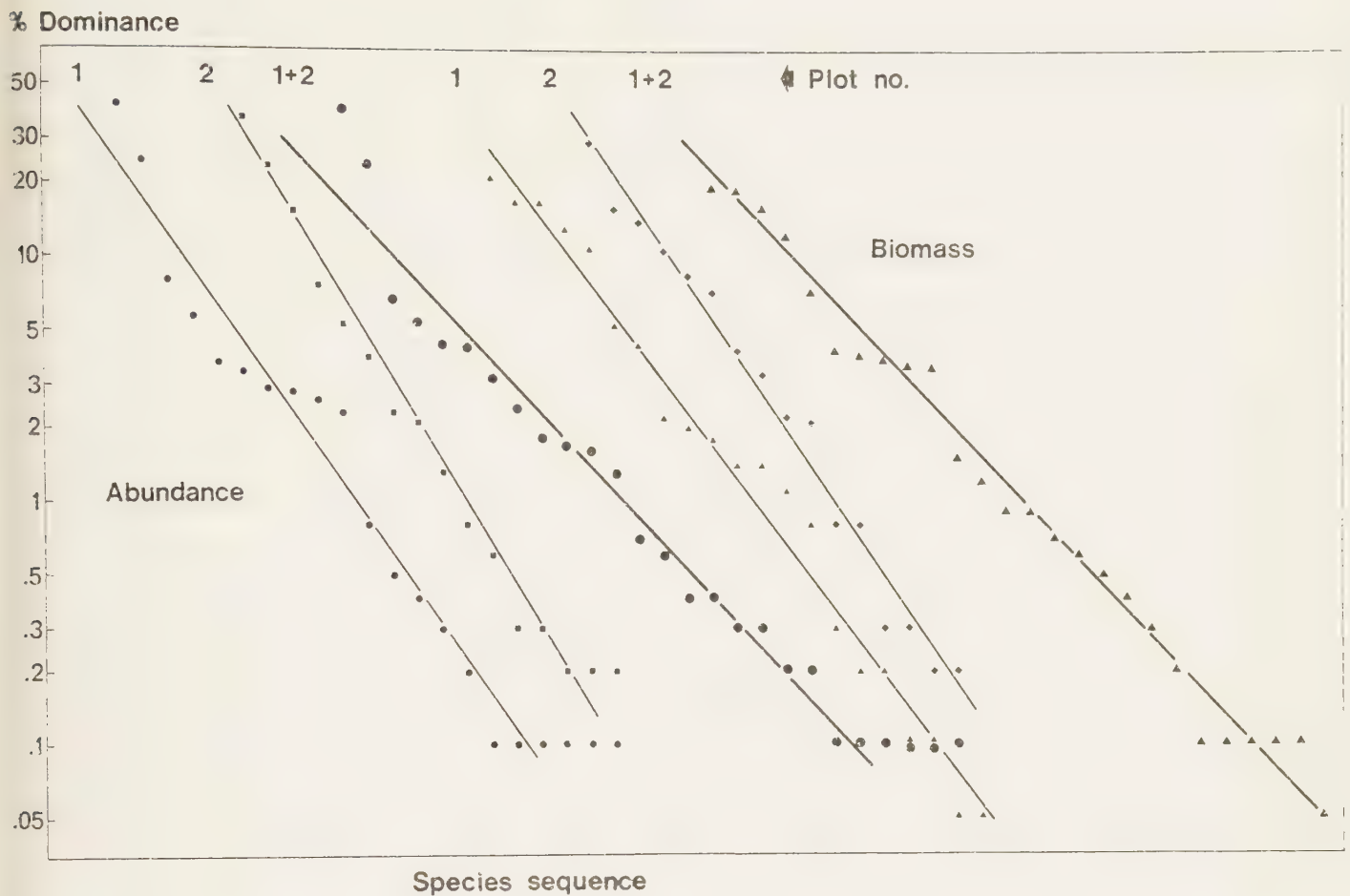


Fig. 5. Species dominance plots for the communities of K1 and K2 at Ammarnäs. The three lines to the left show percent abundance and the three to the right percent biomass.

% Dominance Abundance

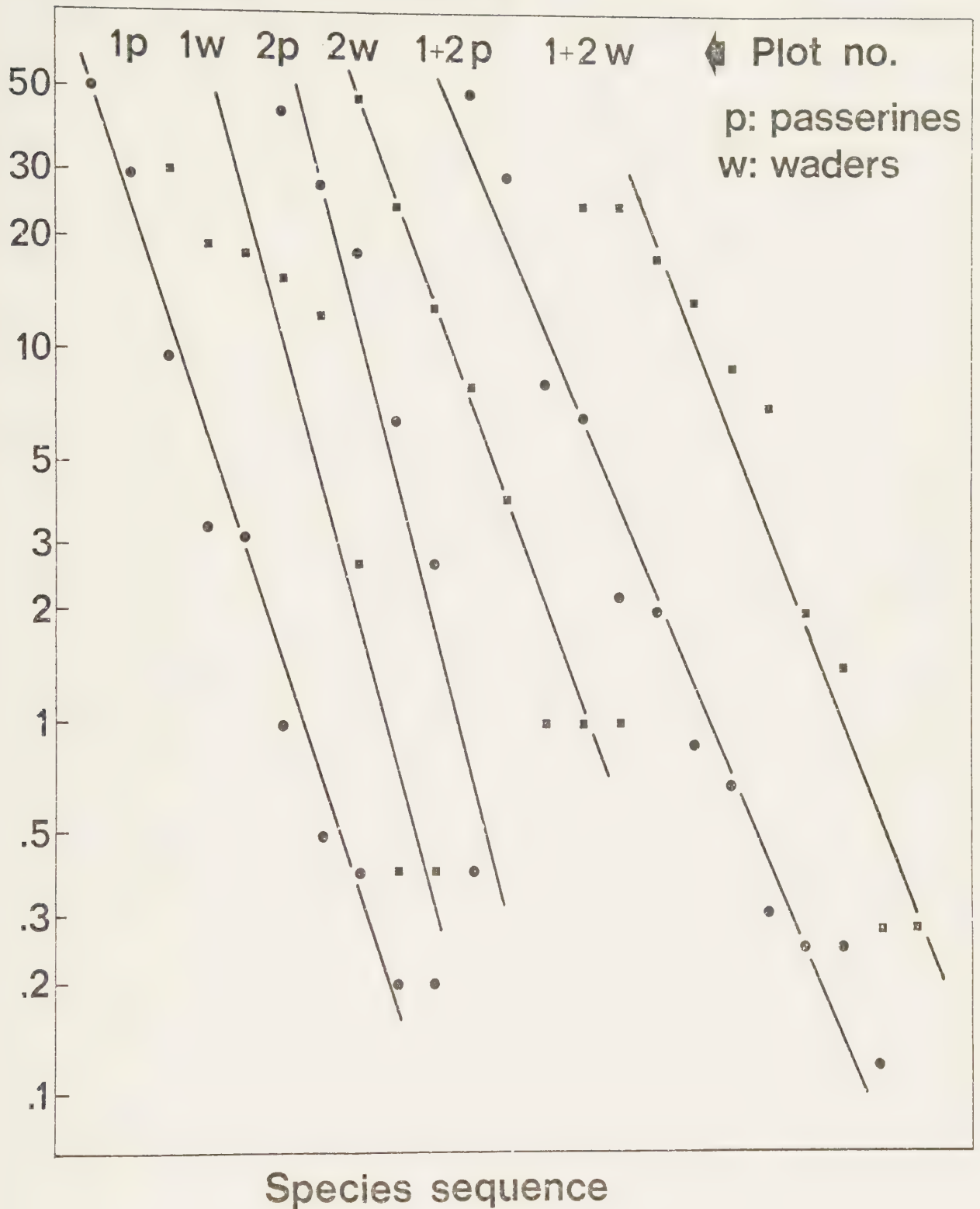


Fig. 6. Species dominance curves for passerines and waders separately in study plots K1 and K2.

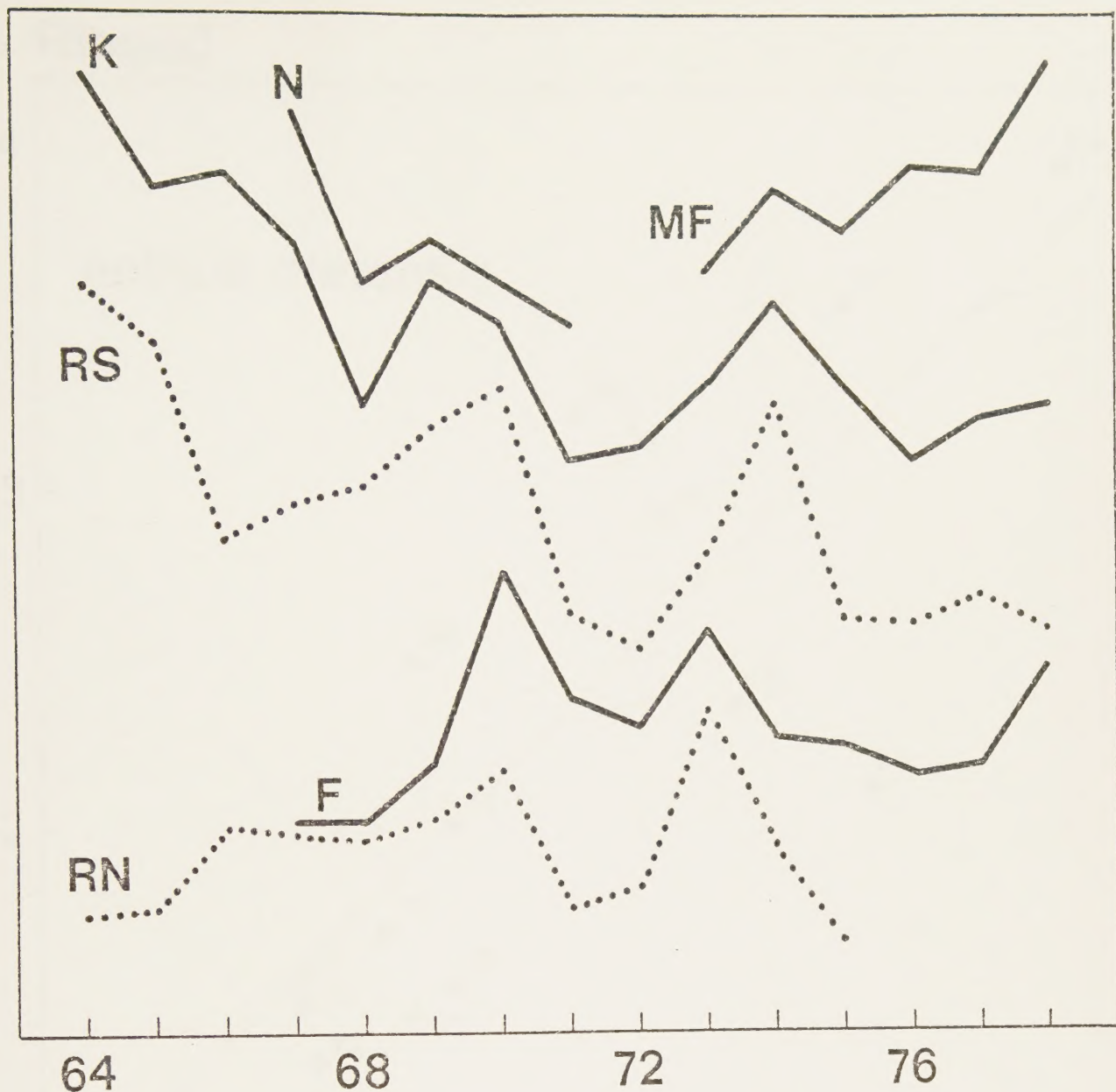


Fig. 7. Fluctuations of *Anthus pratensis* populations. K = the Ammarnäs study plots K1 and K2, N = Nedal (Moksnes 1973), MF = visible migration at Falsterbo (Roos, in litt.), F = Finse (Stenseth 1979), RS and RN = ringing totals for Sweden and Norway.

% Ringed

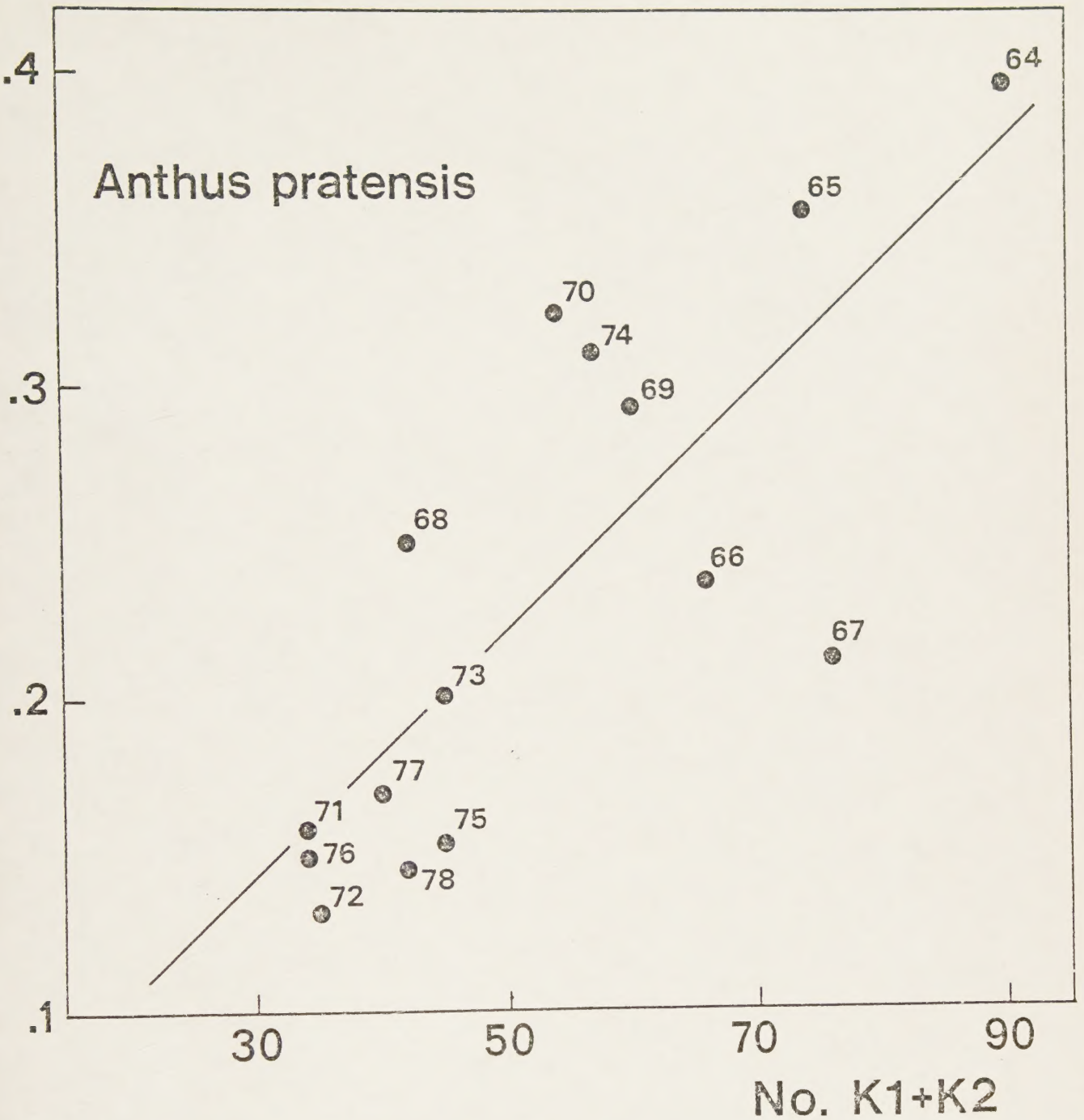


Fig. 8. Correlation between the number of *Anthus pratensis* breeding in the Ammarnäs plots K1 and K2 and the number ringed in all Sweden (expressed as percent of the total number of birds ringed). The correlation coefficient is 0.79.

